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Smells familiar: group-joining decisions of predatory mites are mediated by olfactory cues of social familiarity

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Group-living animals frequently have to trade off the costs and benefits of leaving an established group and joining another group. Owing to their high fitness relevance, group-joining decisions are commonly nonrandom and may be based on traits of both individual members and the group such as life stage, body size, social status and group density or size, respectively. Many group-living animals are able to recognize and to associate preferentially with familiar individuals, i.e. those encountered before. Hence, after dispersing from established groups, animals commonly have to decide whether to join a new familiar or unfamiliar group. Using binary choice situations we assessed the effects of social familiarity on group-joining behaviour of the plant-inhabiting predatory mite *Phytoseiulus persimilis*. Group living in *P. persimilis* is brought about by the patchy distribution of its spider mite prey and mutual conspecific attraction. In the first experiment, gravid predator females given a choice between spider mite patches occupied by unfamiliar and familiar groups of females strongly preferred to join familiar groups and to deposit their eggs in these patches. Preference for socially familiar groups was robust across biases of spider mite prey densities between choice options. The second experiment revealed that the predatory mite females can smell social familiarity from a distance. Females subjected to odour choice situations in artificial cages were more strongly attracted to the odour of familiar than unfamiliar groups. We argue that *P. persimilis* females preferentially join socially familiar groups because a familiar social environment relaxes competition and optimizes foraging and reproduction.

Group living is a ubiquitous phenomenon in animals (Krause & Ruxton 2002: Earley & Dugatkin 2010). Widespread individual benefits of group living are, for example, enhanced vigilance, increased foraging success, reduced predation risk, or more mating opportunities and higher reproductive success. However, group living may also incur costs such as increased competition for shared resources and mates or increased disease transmission (Krause & Ruxton 2002; Earley & Dugatkin 2010). Individuals of group-living species are usually not permanently associated with a given group but are frequently faced with decisions to leave an established group and either join the next available one or search for another. Joining behaviour is defined as the nontransient association of a previously solitary individual with a given group (Prokopy & Roitberg 2001). Proximately, group-joining decisions may be based on diverse sensory modalities such as olfaction (Borden 1985; Campbell et al. 1993), vision (Langbein et al. 2004) or audition (Wijenberg et al. 2008). Ultimately, individuals should have evolved abilities to recognize and join those groups that provide the highest net fitness gains (Prokopy & Roitberg 2001; Krause & Ruxton 2002; Reddon et al. 2011). Accordingly, the trade-off between the costs and benefits of joining a given group poses a major challenge for group-living animals (Krause & Ruxton 2002; Earley & Dugatkin 2010).

The costs and benefits of joining a given group may depend on numerous interrelated traits at the individual and group level such as member life stage and body size (Ranta et al. 1992), competitive ability (Metcalfe & Thomson 1995), dominance hierarchy (Jordan et al. 2010), genetic relatedness (Ward & Hart 2003), social familiarity (Griffiths et al. 2004) or group size and density (Barber & Wright 2001). Accordingly, group-joining decisions may be based on various morphological, physiological, behavioural or ecological characteristics of a given group and its members, respectively.

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Owing to the high fitness relevance of social interactions, many group-living animals have evolved sophisticated abilities to assess the social status of group members such as the ability to discriminate unfamiliar from familiar individuals, that is, those with whom they interacted previously (Mateo 2004). Use of social familiarity for group-living decisions is known from both vertebrates and invertebrates and is especially well documented for fish (Brown & Colgan 1986; Miklosi et al. 1992; Brown & Smith 1994; Barber & Wright 2001; Jordan et al. 2010) but has also been observed in cattle (Hagen & Broom 2003), birds (Senar et al. 1990), mice (Szenczi et al. 2012), lizards (Moreira et al. 2008), cockroaches (Wijenberg et al. 2008), ants (Wilgenburg van 2007) and mites (Strodl & Schausberger 2012a, b, 2013; Zach et al. 2012). Social familiarity may allow better coping with the interrelated cognitive, behavioural and physiological challenges inherent to group living and thus optimize the group-living benefits. Potential advantages of preferential association with familiar individuals include foraging benefits (Dugatkin & Wilson 1992; Ward & Hart 2005; Strodl & Schausberger 2012a), improved antipredator behaviours (Chivers et al. 1995; Strodl & Schausberger 2012b), more effective transmission of information (Swaney et al. 2001), less intense competition for food (Metcalfe & Thomson 1995; Utne-Palm & Hart 2000), enhanced reproductive success (Strodl & Schausberger 2013) or facilitation of reciprocal behaviours (Croft et al. 2005; Zach et al. 2012).

In this study we assessed the influence of social familiarity on group-joining behaviour of the plant-inhabiting predatory mite *Phytoseiulus persimilis*. This species is a highly specialized predator of tetranychid mites such as the herbivorous two-spotted spider mite *Tetranychus urticae*. The spider mites are patchily distributed on their host plants and so are *P. persimilis* foraging, reproducing and developing in the spider mite patches (Sabelis 1985). In the prey patches the predators frequently encounter each other, providing opportunities to become familiarized with one another. Contact early in life, in the larval stage preceding the two nymphal stages, seems crucial for familiarization, with imprinting being an important learning mechanism used (Schausberger 2004, 2007; Strodl & Schausberger 2012a, b). The ability of *P. persimilis* to discriminate familiar from unfamiliar conspecifics, independent of genetic relatedness, has been observed in various contexts such as cannibalism (Schausberger 2007), within-group association, foraging and reproduction (Strodl & Schausberger 2012a, 2013), dispersal (Zach et al. 2012) and antipredator behaviour (Strodl & Schausberger 2012b). Close genetic relatedness is not a prerequisite for social familiarity but may add indirect fitness benefits, increasing inclusive fitness (Hamilton 1964a, b). The within- and between-plant distribution of *P. persimilis* is spatially and temporally dynamic (Nachman 1981, 2001), albeit not as pronounced as in fission–fusion societies, which are characterized by frequent merging, splitting and exchanging among groups such as shoaling fish (e.g. Croft et al. 2005). Prey patch residence and leaving decisions of *P. persimilis* are known to depend mainly on prey availability and competitor presence (e.g. Nachman 1981, 2001) but nothing is known about whether intraspecific behavioural traits such as social familiarity play a role in their group formation and joining dynamics. We conducted two experiments to assess whether social familiarity affects group-joining decisions of adult *P. persimilis* females. In the first experiment, gravid females were given a choice between spider mite prey patches occupied by unfamiliar and familiar females and their residence and oviposition preferences were assessed. Based on the results of the first experiment, in the second experiment we examined whether the predatory mite females respond to volatile chemosensory cues released by the familiar and unfamiliar groups.

METHODS

Origin and Rearing of Experimental Animals

Experimental animals were obtained from females drawn from a laboratory-reared population of *P. persimilis*, originally founded about 4 years ago with specimens field-collected in Valencia, Spain. The population was maintained on artificial rearing units each consisting of a plastic tile resting on a water-saturated foam cube (130 × 130 mm), placed in a plastic box (200 × 200 mm) half-filled with water and surrounded by water-saturated tissue paper. The predatory mites were fed with mixed life stages of *T. urticae*, reared on whole bean plants, *Phaseolus vulgaris*, by adding detached spider mite-infested leaves onto rearing units in 2–3-day intervals. Rearing units were stored at 25 ± 1 °C, 60 ± 5% relative humidity and 16:8 h light:dark.

Familiarization of P. persimilis

Arenas used to obtain predator eggs of similar age and subsequently to generate familiar individuals (familiarization arenas) consisted of single bean leaves placed adaxial surface down on a water-saturated foam cube (50 × 50 mm) in a small plastic box (100 × 100 mm) half-filled with water. Strips of tissue paper folded over the edges of the leaves prevented the mites escaping. Before adding the predators, we brushed mixed life stages of *T. urticae* onto the arenas. Each familiarization arena was furnished with six to eight gravid *P. persimilis* females, randomly drawn from the rearing units, and allowed to lay eggs for 24 h. After 24 h, the predator females were removed and their offspring reared to adulthood. Gravid females to be used in the experiment were randomly chosen from this arena and marked with a tiny watercolour dot on their dorsal shield for identification during the experiment. Familiar females, that is, those reared on the same familiarization arena, were marked with the same colour, but colours differed between familiarization arenas.

Experiment 1: Group-joining Decisions

Binary choice experiments were conducted to assess the influence of social familiarity on group-joining decisions of gravid *P. persimilis* females. Each experimental arena consisted of a pair of similarly sized leaflets, taken from trifoliate bean leaves, connected by a wax bridge. The leaflets, with the adaxial surface down and their bases facing each other, were placed about 40 mm apart on moist tissue paper covering a water-saturated foam cube (160 × 80 mm and 80 mm high), placed in a plastic box (200 × 100 mm and 100 mm high) half-filled with water. Each leaflet had an accessible area of 40 × 40 mm created by folding strips of moist tissue paper over the edges of each leaflet. The wax bridge (about 40 × 10 mm) connecting the two leaflets was created by dripping hot wax from a nonfragrant candle on the tissue paper (Vanas et al. 2006).

To provide sufficient prey eggs for the predators on the choice leaflets, 1 day before the predators were released we placed, on each pair of leaflets, 7–12 gravid *T. urticae* females, depending on the number of prey eggs needed for the experiment. After 24 h the *T. urticae* females were removed, the number of eggs laid was counted, and the required number of prey eggs was left on the leaflets according to the design of the experiment. If the number of spider mite eggs was above or below the required amount, eggs were removed or added using a fine camel hair brush. To assess the influence of prey density on the joining decisions of *P. persimilis*, we tested seven ratios of prey egg densities between the two leaflets, harbouring the familiar and unfamiliar females, respectively:

balanced (70:70 to 90:90 eggs), slightly biased to unfamiliar or familiar (75:100 and 100:75 eggs), moderately biased to familiar or unfamiliar (75:125 and 125:75 eggs), and strongly biased to familiar or unfamiliar (75:150 and 150:75 eggs). Prey egg density in the balanced design was chosen to allow maximum egg production of each predator female within the 24 h experimental period (Vanas et al. 2006).

Before starting the experiment, we placed three randomly selected familiar gravid females on each leaflet of a pair. Predators placed on two opposite leaflets came from two different familiarization arenas; hence, the predator females were familiar within each leaflet but unfamiliar between leaflets. After 15 min, a gravid unmarked female (henceforth termed the experimental female) that was familiar with the females of one of the two groups but unfamiliar with the females of the other group was released at the base end of the T-shaped wax bridge and allowed to join one of the two groups. Subsequently, the position of the experimental female and the number of eggs laid by the predators on each leaflet were recorded immediately after release, and then again after 30, 60, 90, 120, 150, 360 and 1440 min. Occasionally, and especially towards the end of the experiment in the moderately and strongly biased designs (see below), the marked females started to move between the two leaflets. Therefore, we excluded from analyses position and oviposition data of the experimental female at observation points where the distribution of the marked females deviated from the original distribution, which happened in <3% of all observations. Thirty replicates were run for the balanced design and 20 for each of the biased designs.

Experiment 2: Group Recognition by Olfaction

In experiment 2, we examined whether gravid *P. persimilis* females are able to distinguish between the smell of socially familiar and unfamiliar groups. Each experimental set-up consisted of a group cage and a choice cage (Fig. 1a), fixed together with the group cage bottom side up and the choice cage bottom side down (Fig. 1b). Each cage was meticulously cleaned with 75% ethanol on the day before the experiment took place.

Each group cage consisted of two separate circular cells (diameter 15 mm, spaced 15 mm apart) in an acrylic plate covered by gauze on the bottom side and by a removable microscope slide on the upper side (Fig. 1a; Schausberger 1997). Before the experiment, three familiar females, randomly chosen from the same familiarization arena, were placed in each cell of the group cage. The females were familiar within each cell but unfamiliar between the two cells of a cage. Each choice cage had two cells in the same position as the group cage but, in contrast to the group cage, the two large cells were connected by a T-shaped aisle leading to a small cell at the bottom end of the T (Fig. 1a; Schausberger & Hoffmann 2008). Like the group cage, the choice cage was closed on the bottom side by gauze and on the upper side by a microscope slide. The small cell was used as the release site of the experimental female. Having gauze on the bottom sides of both the group and choice cages prevented any direct contact between the females and their products in the group cage and the experimental female released in the choice cage. Placement of the group cage below the choice cage with their gauze sides facing each other allowed diffusion of volatiles from the females or their products from their respective group cage cell into the corresponding choice cage cell (Fig. 1b). After 30 min acclimatization of the females in the group cage, the experiment was started by releasing the experimental female, which was familiar with the females residing in one of the two cells of the group cage, in the small cell of the choice cage. Her position (in one of the large cells or somewhere else, considered the neutral zone) was recorded immediately after release (first choice), and then after 20, 40, 60, 80, 100 and 120 min. Thirty individual females were tested for their olfactory group preferences. Each female and choice/group cage arrangement was used only once.

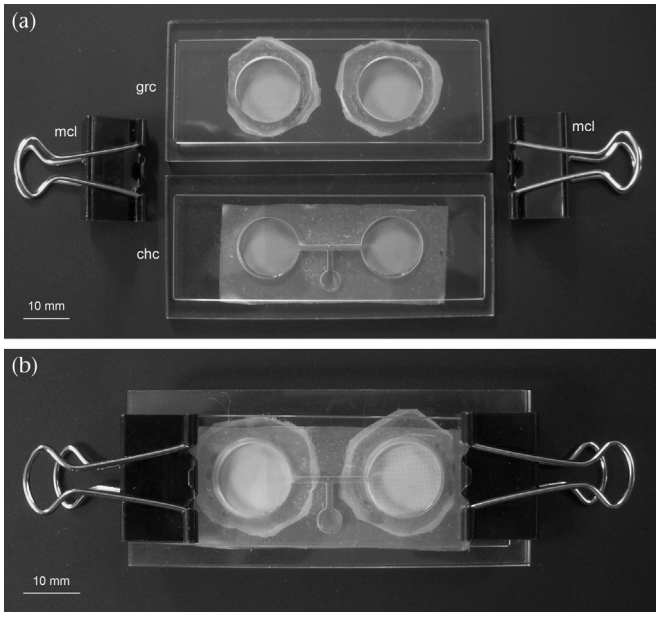

Figure 1. Set-up of group (grc) and choice (chc) cages used in the experiment on olfactory group recognition by single *P. persimilis* females, with components separate in (a) and assembled (top view) in (b). Each group (grc) and choice (chc) cage basically consisted of two large circular cells (each 15 mm diameter, spaced 15 mm apart) laser-cut into an acrylic plate (3 mm thick). The cells were covered by gauze on the bottom side and by a removable microscope slide on the upper side. In the group cage the two large cells were separate while in the choice cage they were connected by a T-shaped aisle leading to a small cell at the bottom end of the T (chc), used as release site for the experimental *P. persimilis* female. Each cell of the group cage contained three females, with the females in one cell being familiar and those in the other cell being unfamiliar to the experimental female released in the choice cage. During the experiment, the group and choice cages were assembled (b), fixed by metal clamps (mcl), with the group cage bottom (gauze) side up and the choice cage bottom (gauze) side down, allowing diffusion of volatiles from the females in the cells of the group cage to the corresponding cells of the choice cage.

Statistical Analyses

All data were analysed using SPSS 18.0 for Windows (SPSS Inc., Chicago, IL, U.S.A.). In both experiments 1 and 2, and in experiment 1 within each of the seven ratios of spider mite densities between the two leaflets, we used Wilcoxon signed-ranks tests to assess whether the aggregated positions of the experimental females on the familiar and unfamiliar side differed from each other. To this end, we first calculated the aggregated position of each female, that is, the number of times she was observed on the familiar and unfamiliar side. We used generalized estimating equations (GEE, Hardin & Hilbe 2003; binomial distribution, logistic link, autocorrelation structure between observation points) to analyse in experiment 1 whether the preference for the familiar side differed between spider mite availability distributions over time (used as nested term), and in experiment 2 whether the preference for the familiar group changed over time. The number of predator eggs deposited within 24 h in the balanced prey density design of experiment 1 was compared between the familiar and unfamiliar side by a *t* test for dependent samples.

RESULTS

Experiment 1: Group-joining Decisions

Regardless of whether prey density was balanced between the two connected leaflets or biased towards the familiar or unfamiliar

group, *P. persimilis* females had a highly significant preference for joining the familiar group (Wilcoxon signed-ranks tests: $P \leq 0.001$ for each prey ratio; balanced: $N = 30$, $Z = -3.435$; slightly biased to unfamiliar: $N = 20$, $Z = -3.578$; slightly biased to familiar: $N = 20$, $Z = -4.025$; moderately biased to unfamiliar: $N = 20$, $Z = -3.578$; moderately biased to familiar: $N = 20$, $Z = -4.025$; strongly biased to unfamiliar: $N = 20$, $Z = -3.628$; strongly biased to familiar: $N = 20$, $Z = -4.025$; Fig. 2). Overall, attraction to socially familiar groups was not counterbalanced by attraction to and/or arrestment at higher prey densities. Preference for joining the familiar group did not differ between the seven prey density ratios (GEE: Wald $\chi^2_6 = 3.548$, $P = 0.738$) and did not change over time (Wald $\chi^2_3 = 5.275$, $P = 0.153$; Fig. 2). In the balanced prey density design, the preference of the experimental female to join the familiar group resulted in a higher total number of predator eggs produced on the familiar (mean ± SE: 9.1 ± 2.7) than unfamiliar side (7.2 ± 2.8; *t* test for dependent samples: $t_{28} = 3.834$, $P = 0.001$), indicating alignment of joining and oviposition site preferences of the experimental female.

Experiment 2: Group Recognition by Olfaction

Across all observation points *P. persimilis* females had a highly significant preference for the smell emanating from the familiar group (Wilcoxon signed-ranks test: $Z = -4.571$, $N = 30$, $P \leq 0.001$). The preference for the smell of the familiar group did not change over time (GEE: Wald $\chi^2_6 = 3.082$, $P = 0.799$; Fig. 3).

DISCUSSION

Our study demonstrates that group-joining decisions of the predatory mite *P. persimilis* are governed by social familiarity. In choice situations, gravid females strongly preferred to join familiar conspecific groups and deposited their eggs in prey patches occupied by familiar females. Preference for socially familiar groups was stronger than preference expected from prey density alone, that is, at the same conspecific group size attraction to socially familiar groups in low prey density patches outweighed attraction to socially unfamiliar groups in high prey density patches.

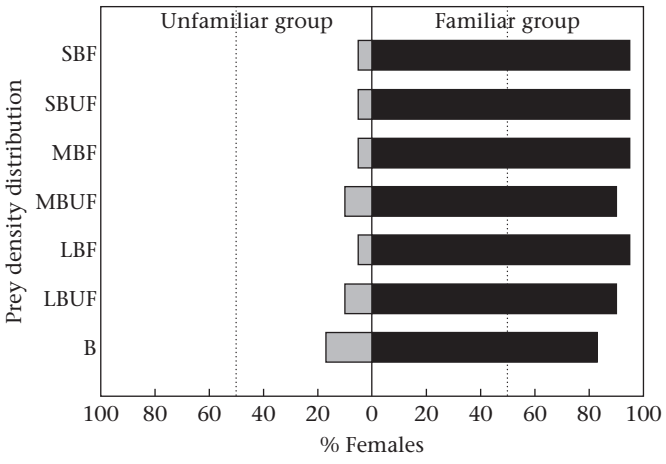

Figure 2. Joining behaviour of single *P. persimilis* females given a choice between two spider mite-infested leaflets occupied by a familiar and an unfamiliar group of conspecific females. Each conspecific group consisted of three gravid females. The ratio of prey egg densities between the leaflets harbouring the familiar and unfamiliar group was either balanced (B), slightly biased to the unfamiliar (LBUF), slightly biased to the familiar (LBF), moderately biased to the unfamiliar (MBUF), moderately biased to the familiar (MBF), strongly biased to the unfamiliar (SBUF), or strongly biased to the familiar (SBF) group. The dotted lines depict the predicted fractions of *P. persimilis* joining the familiar or unfamiliar group under random choice.

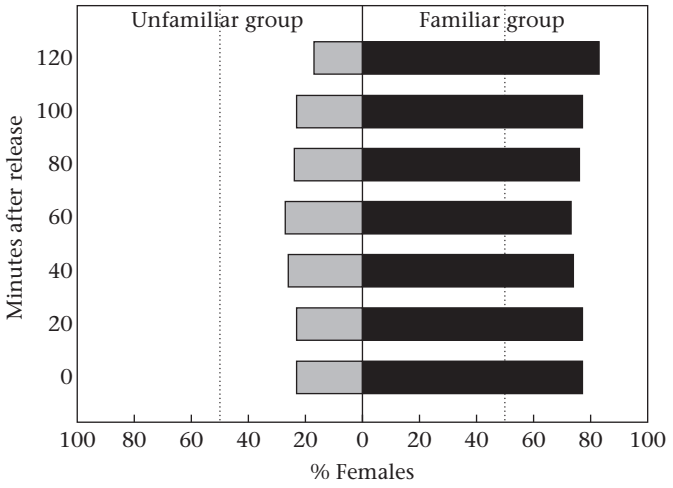

Figure 3. Olfactory group recognition by single *P. persimilis* females given a choice between the odours of a socially familiar and an unfamiliar group of conspecific females in artificial cages over time. The dotted lines depict the predicted fractions of *P. persimilis* joining the familiar or unfamiliar group under random choice.

The second experiment suggests that the experimental predatory mite females were attracted to the conspecific groups from a distance, mediated by volatiles emanating from the bodies or the products of the group members. This finding is corroborated by the observation in the first experiment of most females moving immediately to the familiar group after release. Like all mites of the family Phytoseiidae, *P. persimilis* is eyeless and orients itself mainly by chemosensory cues (Sabelis & Dicke 1985). This is also true for social interactions. Previous studies and observations (Zhang & Sanderson 1992; Schausberger & Croft 2001; Schausberger 2007; Strodl & Schausberger 2013) revealed the involvement of tactile or close range (less than one body length) volatiles in social recognition of *P. persimilis*. Analogous to olfactometer results on conspecific attraction in *P. persimilis* by Janssen et al. (1997), our study reveals the involvement of medium-range volatiles: in experiment 2 the distance to the odour source was >30 times the body length of the predators (0.4–0.5 mm). These odours were not general in their composition but highly specific allowing them to mediate group-joining decisions. The chemistry of the cues mediating social interactions in *P. persimilis* is unknown but the chemical signatures indicating familiarity may emanate directly from the body, as in insects (Howard & Blomquist 2005) or fish (Brown & Smith 1994), or from metabolic waste products (e.g. Moreira et al. 2008 for lizards) or footprints left by the predators on the substrate, or a combination thereof.

In principle, the responses of *P. persimilis* in tritrophic contexts such as in experiment 1 can be affected by a number of factors such as leaf age (Takabayashi et al. 1994), herbivore density (Maeda & Takabayashi 2001) or damage level (Nachappa et al. 2006). However, within each choice situation of experiment 1, the two choice options were completely the same with respect to leaf age and size, and, in the balanced design, completely the same with respect to prey density and damage level. The only difference was social familiarity of the experimental female to one of the two conspecific groups, and, only in the biased designs, the prey densities. In the biased designs, the two leaf discs were slightly differently damaged and furnished with different numbers of spider mite eggs together with different amounts of webbing and faeces deposited by the spider mite females during feeding and oviposition. Despite differing damage levels we assume that possible volatiles emitted by the leaf discs did not differ markedly between the two sides because the leaves were detached from the plant and it takes >24 h

until plants change their volatiles after spider mite infestation (e.g. Maeda & Takabayashi 2001). The spider mite eggs do convey information via tactile chemosensory cues (Hoffmann et al. 2011) and, when present on leaves, may also emit volatiles attracting *P. persimilis* from a distance (Sabelis et al. 1984). Similarly, the webs containing the faeces of the spider mites have an arresting effect on the predators (e.g. Schmidt 1976) but may also attract the predators from a distance (Sabelis et al. 1984). Low volatility of the chemical cues present in/on the spider mite webbing, faeces and eggs may partly explain why the preference to join the familiar group did not change despite prey densities being strongly unbalanced. None the less, given that such volatile kairomones do exist, it is remarkable that attraction to socially familiar groups outweighed attraction to higher prey densities. In a similar vein, attraction to social cues outweighed attraction to favourable abiotic habitat factors, such as shelter characteristics, in group-living cockroaches (Jeanson & Deneubourg 2007) and woodlice (Devigne et al. 2011).

We argue that the observed group-joining preferences of *P. persimilis* females are adaptive. Although the design of our experiments did not allow us to quantify fitness benefits it has been shown before that association with familiar individuals relaxes food competition and enhances reproduction compared with association with unfamiliar females (Strodl & Schausberger 2013). Other benefits of social familiarity for *P. persimilis* include faster reaction times to predator attacks, owing to relaxation of shared attention constraints (Strodl & Schausberger 2012b), and optimized foraging (Strodl & Schausberger 2012a), patch exploitation and dispersal (Zach et al. 2012). These benefits accrue independently of the level of genetic relatedness between group members in *P. persimilis* and other animals such as fishes (Griffiths et al. 2004, Ward & Hart 2005), birds (Senar et al. 1990) and mammals (Takeda et al. 2003), underlining the significance of social familiarity as a selective force of group living.

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